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A POPULATION STUDY OF THE NEOTROPICAL NYMPHALID BUTTERFLY, *ANARTIA AMALTHEA*, IN ECUADOR

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The population biology of the southern Neotropical butterfly *Anartia amalthea* (Nymphalidae, Nymphalinae) has not been previously described. However, some work has been done on its northern tropical allied form, *A. fatima* (Emmel, 1972). The present study of *A. amalthea* will allow for initial comparisons to be made between this species and its northern allied form. Reported here are data obtained on population size, intrapopulation movement, and social interaction in a population of *A. amalthea* located in the eastern lowlands of Ecuador.

MATERIALS AND METHODS

Anartia amalthea inhabits rain forest areas ranging from the lowlands of Panama southward throughout the lowlands of South America to southern Brazil (Godman and Salvin, 1879). It is a deliberate-flying, medium-sized butterfly with a wingspread of approximately 40 mm. The ground color of the wings dorsally is dark brown to black and there are usually three red spots of variable size located at the basal portion of the hindwing. Both sexes bear a red (male) or orange (female) median band running across both the forewing and hindwing with a series of white spots (usually twelve) near the apex and postmedian area of the forewing (Fig. 1-4). The ventral side is almost identical in pattern but much lighter in general aspect. In many cases the sex of the individual was difficult to determine strictly by color characteristics. Despite the abundance of the species throughout the neotropics, the life history and larval food plants, undoubtedly weedy second-growth species, remain unknown (Comstock and Vazquez, 1961). However, in the present study, adult *A. amalthea* were found to be feeding on the mint *Hyptis mutabilis* and a weedy species from the genus *Sida* (Malvaceae).

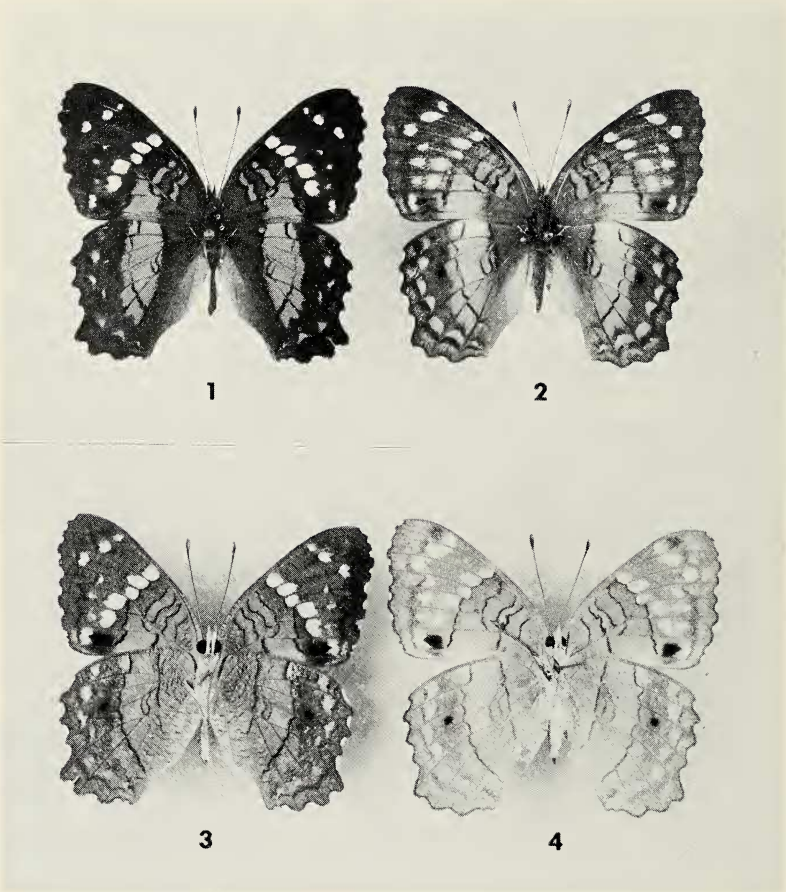

Fig. 1-4.—Photographs of *Anartia amalthea*: (1) Male dorsal surface, (2) female dorsal surface, (3) male ventral surface, and (4) female ventral surface.

The characteristic flight pattern of *A. amalthea* is generally casual. Leisurely, slow-wingbeat flight up to approximately 2 meters above ground level was observed as well as erratic fast flight up to 5 meters above ground level. Once alighted on a surface, usually a wide grass blade or leaf, *A. amalthea* will spread its wings and orient itself toward the sun. With an overcast sky this species, when perched, will spread its wings and orient in a random direction. This behavior has a double purpose: (1) *A. amalthea* can thermoregulate and (2) colors are exposed for possible sexual attraction.

The locality of the study site was a second-growth area within the borders of a missionary station at Limoncocha, situated in the eastern Amazonian rain forest of Ecuador at an elevation of 275 meters (latitude 0.4°S, longitude 77.5°W).

The general vegetational formation of the study site was wet tropical rain forest in an intermediate stage of second-growth recovery. The study area was a vegetational "island" 30 by 35 meters surrounded by open fields on three sides and a road to the north (Fig. 5). *Anartia amalthea* were abundant in this area as well as various species of *Euptychia* (Satyridae).

Approximately half of the study area contained grasses and weeds from 0.1 to 2 meters in height and the other half contained bushes and trees from 2 to 7 meters in height. The butterflies flew above the grass as well as up and over the high bushes. Second-growth plants found in the study area were: *Papaya,* young *Balsa,* Piperaceae, *Heliconia* (Musaceae) plants, Convolvulaceae, and other weedy second-growth species.

The daily weather here was variable. According to weather records kept by the personnel stationed at Limoncocha, temperatures very seldom exceed 90°F; temperatures during the study period ranged between 75° and 90°F. The relative humidity near ground level was relatively constant around 70%, with the possibility of rain any time of the day or night. The sun was shining constantly only one morning, September 10, during the entire study period; on the other dates the sky was either overcast or partly cloudy.

Aside from occasional afternoon observations, most of the research was carried out during the morning between 0830 and 1200 hours. This period was inclusive of the peak flight activity which fell between 1030 and 1200 hours on a sunny day. When overcast, there seemed to be no special time of peak flight activity. *Anartia amalthea* were even observed to be active in a moderate rain. Flight activity would begin around 0600 hours and last until 1800 hours.

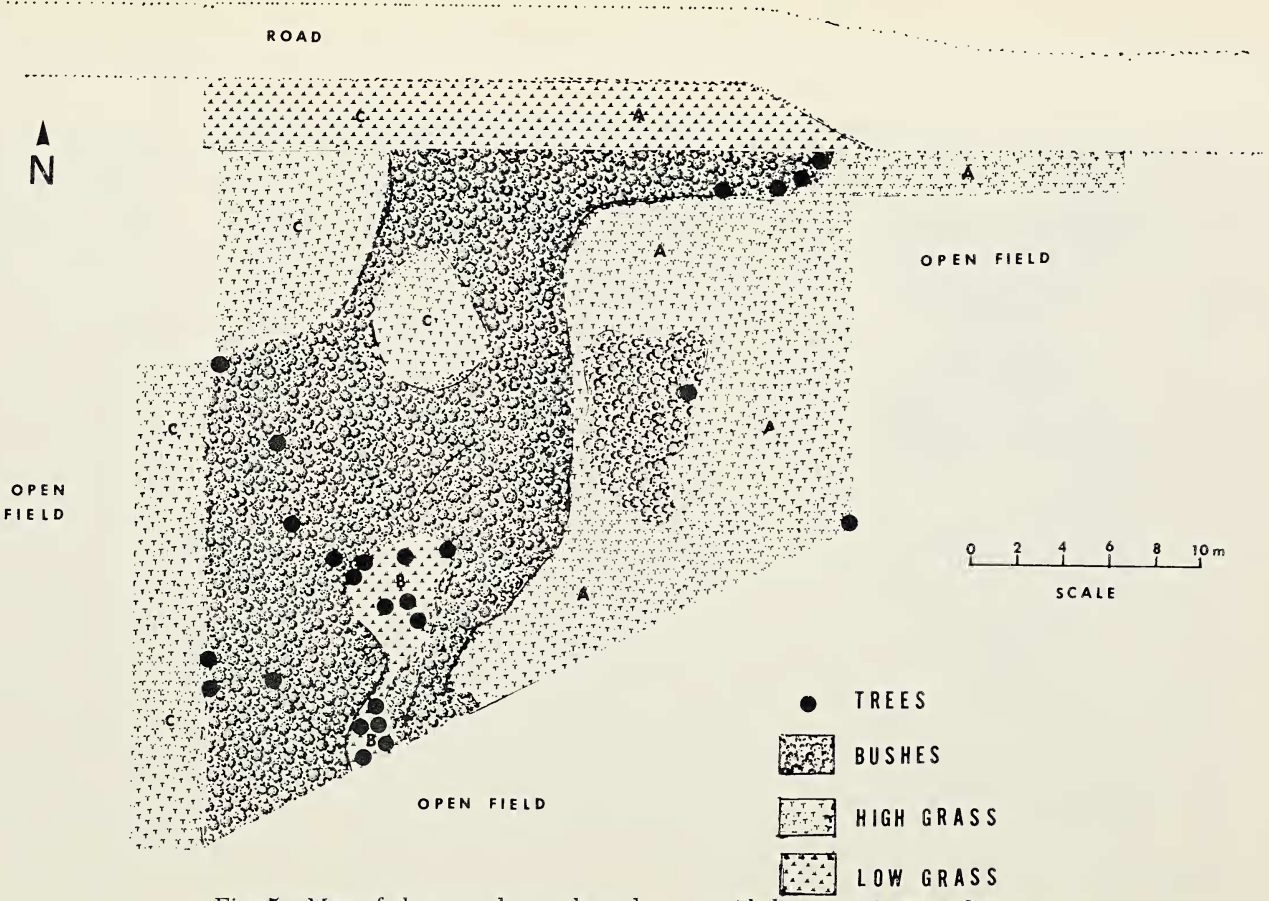

Fig. 5.—Map of the second growth study area with lettering A, B, and C designating the three separate collecting areas.

A capture-mark-release-recapture program to determine population size by three applicable standard methods was initiated on the afternoon of September 5, 1972 and continued until the morning of September 12, 1972. Specimens were marked on the ventral surface of the right wing using a blue Magic Marker pen. Marking was done by coloring in white spots on the wing using a 1-2-4-7-10 coding system (modified from a system first used by Ehrlich and Davidson, 1961) (Fig. 6). Specimens were captured in three separate areas designated A, B, and C (Fig. 5), which are divisions of the entire study area. The purpose of this division was to determine the extent of intrapopulation movement. Each day, work was begun at area A and from there extended to B and C. Collecting time in each area was relatively proportional to the size of the area. In area A collecting time averaged one and a half hours, area B averaged half an hour, and area C averaged one hour. After capture the specimens were marked and put into a holding bag of netting until the alotted capture time had expired. The specimens were released at this time in the area in which they were captured. Recapture procedures also followed the previously stated order.

Several female specimens were marked by coloring in the orange band on the dorsal side of the wing with a red Magic Marker pen. By this procedure the females' band was identical in color to the males. Observations were carried out on these marked females to determine the males' reactions.

RESULTS

The capture-recapture data resulting from this work are summarized by the trellis diagram in Figure 7. Estimates of population size (see Table 1) were obtained with these data using three statistical methods.

1. *Modified Lincoln Index* (Bailey, 1951):

$$P_1 = \frac{(N_2 + 1)\, M_1}{R_2 + 1}$$

where P_1 = population size on day one,
M_1 = the number marked on day one,
N_2 = the total number of captures on day two, and
R_2 = the number of recaptures on day two

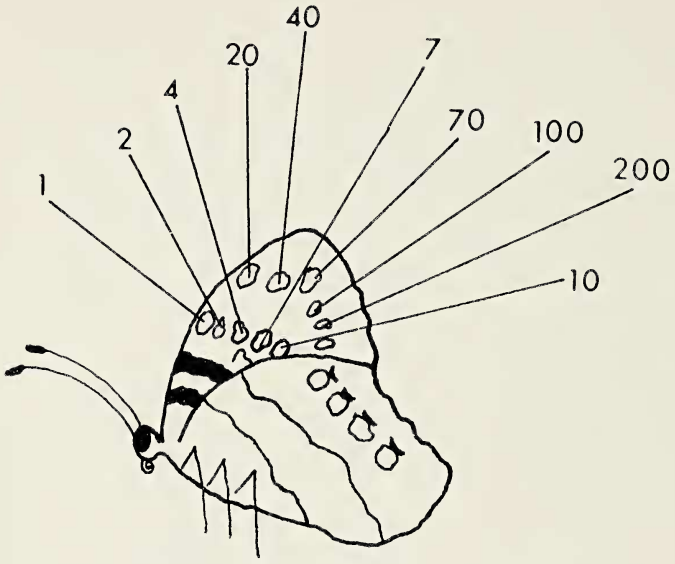

Fig. 6.—*Anartia amalthea*: ventral surface, showing ocellation pattern and coding system.

2. Bailey's *Triple Catch Method* (Bailey, 1952):

$$P_2 = \frac{M_2 \; N_2 \; R_{3_1}}{R_{2_1} \; R_{3_2}}$$

where P_2 = population size on day two,
M_2 = number of individuals marked on day two,
R_{3_1} = number of recaptures taken on day three and marked on day one,
R_{2_1} = number of recaptures taken on day two and marked on day one, and
R_{3_2} = number or recaptures taken on day three and marked on day two

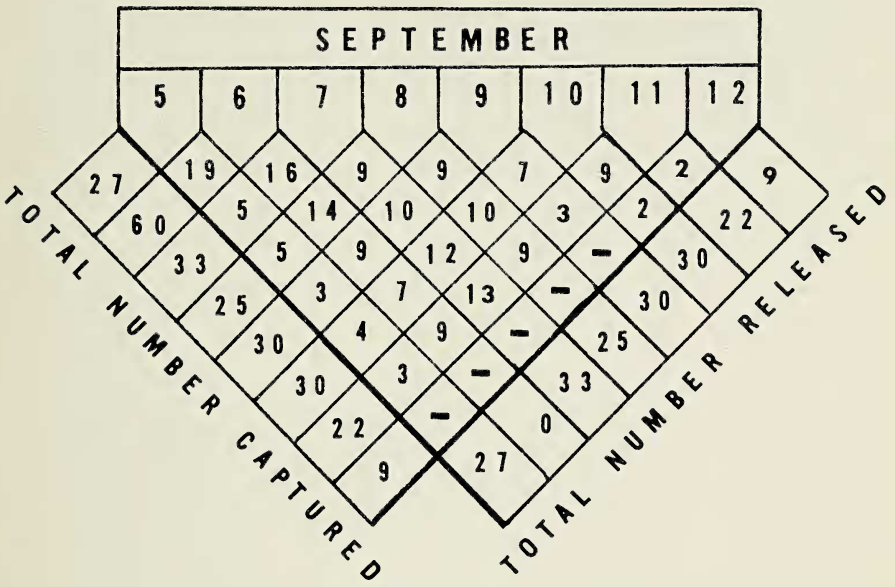

Fig. 7.—Trellis diagram summarizing capture-recapture data on a population of *Anartia amalthea*. On September 5th, for example, 27 adults were captured (left diagonal) and 27 adults were released (right diagonal): 19 of these were recaptured (and released again) on September 6th, 5 were recaptured on September 7th and 8th, 3 were recaptured on the 9th, etc. Dashes indicate no recaptures.

3. *Capture per Unit Effort* method (DeLury, 1947):

$$\frac{\text{No. captured at } t_0}{P_0} = \frac{\text{No. captured at } t_1}{P_1}$$

where P_0 = population size at time 0 and
P_1 = population size at time 1

Population sizes estimated by the above methods were remarkably close on all but two dates, and in agreement with the author's visual estimates of the flying population size. The population varied from 100 to 255 adults using the Modified Lincoln Index and from 78 to 276 adults using the Triple Catch Method (Table 1).

MODIFIED LINCOLN INDEX ESTIMATED POPULATION SIZE	DATE	TRIPLE CATCH METHOD ESTIMATED POPULATION SIZE	CAPTURE PER UNIT EFFORT	
			Percentage Captured	Estimated Population Size
108 adults	September 5	—	25%	–
194 adults	September 6	78 adults	31%	240 adults
161 adults	September 7	173 adults	21%	107 adults
147 adults	September 8	148 adults	17%	122 adults
255 adults	September 9	276 adults	12%	176 adults
201 adults	September 10	96 adults	15%	255 adults
100 adults	September 11	161 adults	22%	147 adults

Table 1.—A summary of the capture-recapture data using three statistical methods: Modified Lincoln Index figures represent the population size on day one. Triple Catch Method figures represent the population size on day two. Capture per Unit Effort figures show the percentage of the estimated population captured each day and the estimated population size that day as determined from the Method's ratio procedure (see text). Modified Lincoln Index estimated population sizes were used to determine percentage of total population captured each day and for P_0 figures in Capture Per Unit effort calculations to determine P_1 on t_1.

	Number of Times Recaptured						
	0	1	2	3	4	5	6
Number of Butterflies Recaptured	108	46	23	13	8	1	1

Table 2.—A summary of the frequencies of recapture for all 200 marked *Anartia amalthea* butterflies. A total of 108 were never recaptured, 46 were recaptured once, 23 recaptured twice, etc.

The Capture per Unit Effort Method assumes that the percentage of the estimated population captured on each date will remain constant if the same unit of effort is exerted each date in sampling. Since this latter requirement was met by the design of the experimental procedure, we may calculate the population size at t_1 by using P_0 estimates determined by one of the other two methods. These figures (Table 1, last column) also show a relatively stable population in this small area of 30 x 35 meters. The Capture per Unit Effort ratios additionally give a good overall picture of the percentage of the total estimated population that was caught each day. Anywhere from 12 to 31% of the actual population present was captured, although within these extremes an average daily capture rate of 20% was normal.

Table 2 gives an overall view of the number of times butterflies were recaptured. The relatively high numbers of recaptures out of the total of 200 butterflies (129 females, 71 males) that were marked and released gives a good idea as to how many of the population are full-time residents. There were 92 out of 200 individuals that were marked and recaptured at least once in areas A, B, and C. Of the 92 recaptured at least once, 46 were recaptured at least once in the same area in which they were marked, 39 were recaptured at least once in another area other than the one in which they were originally marked, and 7 were recaptured at least once in two different areas other than the one in which they were originally marked. These data give a clear indication of the butterflies' restricted movement within a given subarea or only a portion of the whole area, since only 7 out of 92 butterflies moved throughout the 30 x 35 meter area during the eight-day study period.

A mortality curve is developed in Figure 8 by plotting the number of recaptures against the number of days of survival after marking. From this curve the survivorship rate is approximately 7 days. This figure could possibly be larger due to the fact that the study was only carried out for 8 days. A much longer study period would be necessary to determine the exact adult lifetime of *A. amalthea*.

A record was kept each day of the number of males and females captured. Figure 9 shows the daily fluctuation in the percent of females versus the percent of males present in the flying adult population. The sex ratio on a daily basis can also be read from this graph. The high percentage of males on September 8th could be due to the fact that it rained quite hard

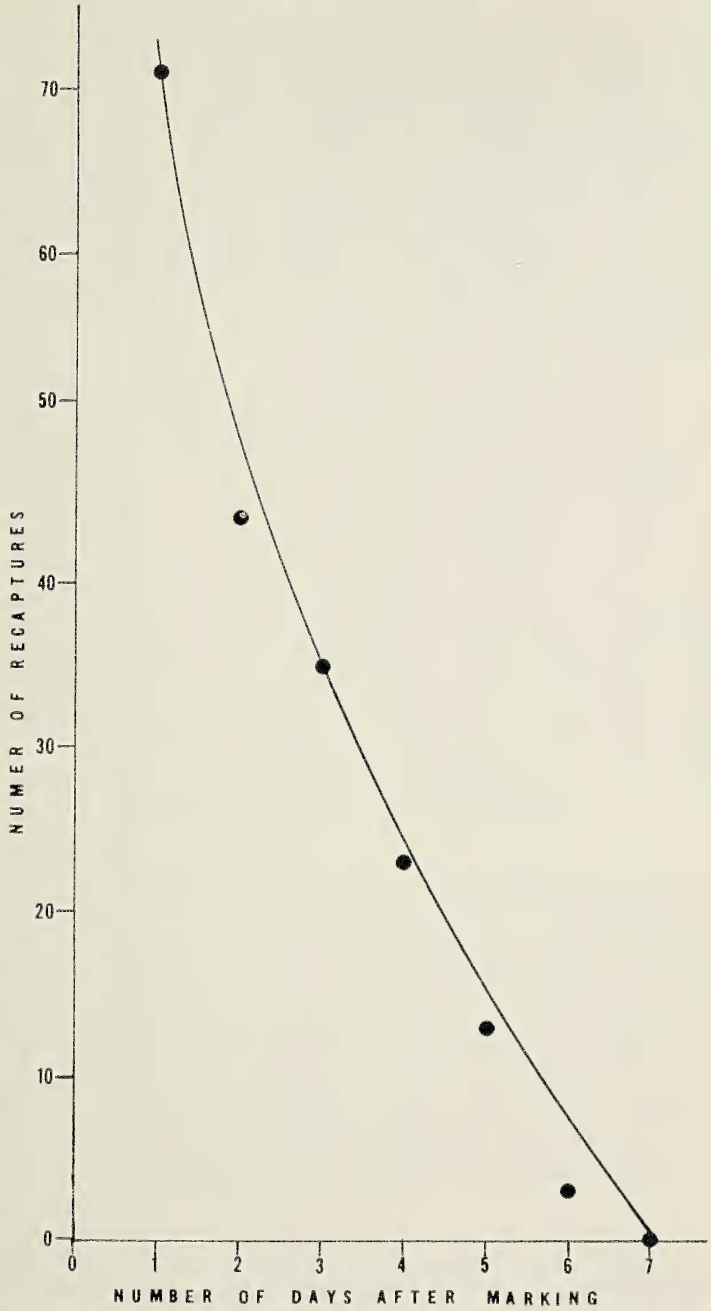

Fig. 8.—The number of recaptured specimens taken on successive days following initial marking. This graph can be read as a survivorship curve with the survivorship of the average adult being approximately 7 days.

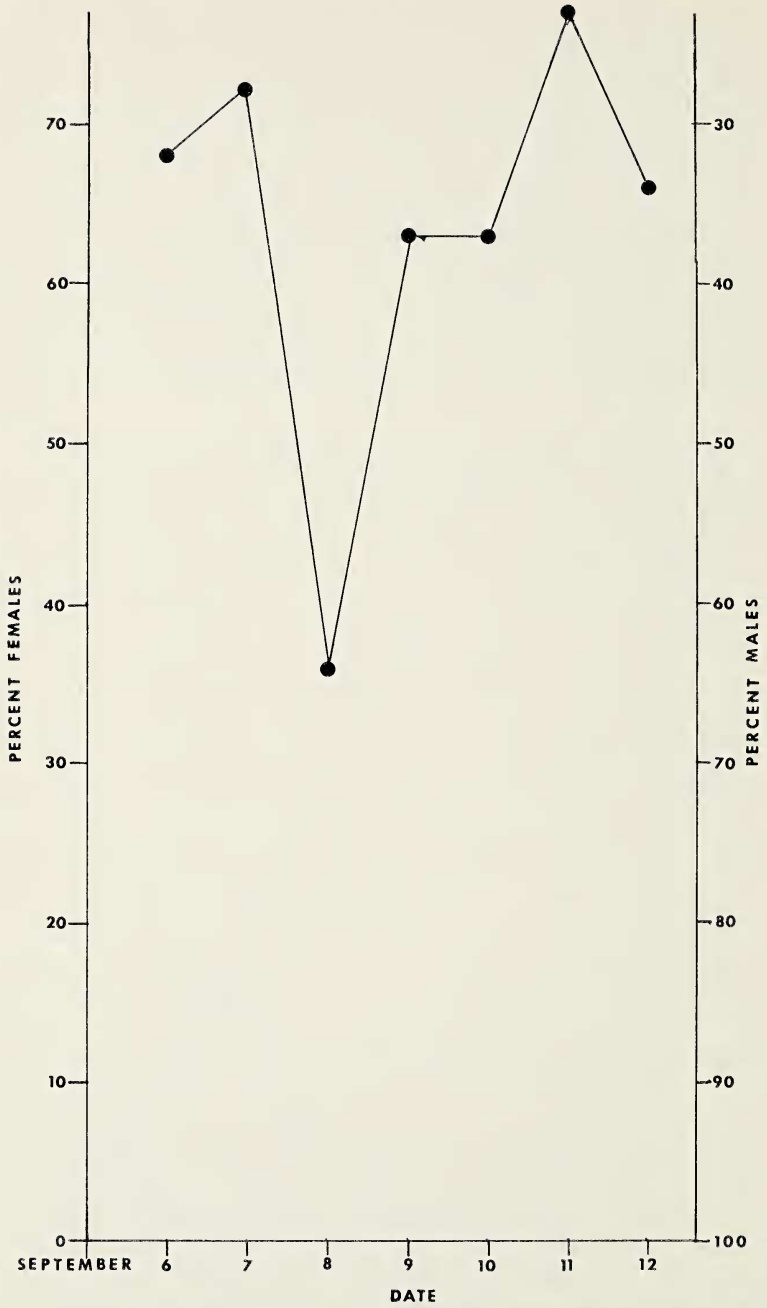

Fig. 9.—Representation of fluctuation in the percentage of females (left axis) and males (right axis) captured.

in the early morning of the eighth; many new males emerged that day after the rain, apparently ahead of a similar large female emergence following a day later. This may be similar to the strategy of various nearctic and other neotropical species of butterflies, where the males commonly emerge at least 24 hours ahead of most females and sperm maturation takes place during the waiting period (T. C. Emmel, personal communication). It would be interesting to know if similar male emergences regularly follow heavy rains. If so, the rains could provide a point of synchrony for male and female reproductive activities and hence increase breeding success. Such selective advantages to synchronize breeding have been hypothesized for tropical butterflies at the onset of the wet season in regions with a seasonal rainfall distribution (Emmel and Leck, 1970). Limoncocha lies in a region with a remarkably uniform distribution of rainfall throughout the year; hence occasional heavy rainstorms may serve the purpose of stimulating emergence in such areas for partly analogous selective reasons (of course, in seasonally wet areas the growth of larval foodplants is also stimulated by the rains and the adults emerge in abundance for this reason, also). Unfortunately for the testing of this hypothesis there were only light rains during the remaining days of this research at Limoncocha, none being as hard as the morning of the eighth. As can be seen from the graph, females were much more abundant than males on every day except the eighth.

DISCUSSION AND CONCLUSIONS

Population size:

The general population size is relatively stable. On very few occasions were there individuals flying out of or through the area observed. Consequently, one would conclude that the population studied is relatively isolated with few individuals entering or leaving the area. Females are predominant with males seemingly only predominant after a very hard rain. Since there is no so-called wet and dry seasons in this particular area, the period after a hard rain is the most opportune time for the emergence of new individuals. The males emerge in great numbers after rains, whereas the females seem to emerge at any time. This would insure a stable, constantly reproducing population.

Intrapopulation Movement

With half of the individuals recaptured at least once in another area other than the area in which they were originally marked, a certain degree of vagility, the ability to cross bar-

riers, is present in this particular species of butterfly. As can be seen from the map in Figure 5 there are natural barriers between areas A, B, and C except for one place along the road between area A and C. Few individuals were captured in this area due to the very low grass and the lack of flowers for feeding. From the data obtained it can clearly be seen that the entire study area should be called a single population of *Anartia amalthea* due to the extent of intrapopulation movement and potential gene exchange. Yet only 7 recaptured specimens actually were found to have moved through all three subareas during the eight-day period.

Social Interaction:

Courtship behavior was observed many times, but no actual mating was observed. Courtship begins with a female perched on a blade of grass or leaf with her wings fully spread. It has been determined that color is one attracting force in butterfly courtship (Crane, 1955). The female having her wings spread in this manner has all her dorsal color pattern exposed to the male. A male flying by the female will swoop in and flutter above the female. The moment the male begins to flutter several inches above the female, she closes her wings and will shift from side to side. This was determined to be a denial to the male. The male will continue fluttering for several seconds and then will fly away, once the female has started the side to side motion. From this it seems that motion is a contributing factor in courtship as described also in *Heliconius erato hydra* (Crane, 1955). No observation of successful courtship was observed.

The females that had their orange band experimentally colored red were observed so as to see the male reaction. These females would display their dorsal surface normally when perched on a blade of grass or leaf. Two cases of interaction between colored females with males were observed. The males would approach the females in the same manner as described previously with no alteration in their behavior. This would indicate that color is not the only determining factor that attracts males to females. The other major alternative factor in courtship behavior would be odor, which has also been determined to be an attracting power in the courtship behavior of certain other South American butterflies (Crane, 1955). These three basic factors which play an important role in courtship—motion, color, and odor—need to be experimentally manipulated in *Anartia amalthea* in a manner similar to that done by Emmel (1972) for the Central American species, *Anartia fatima*.

SUMMARY

Population size, intrapopulation movement, and social interaction were analyzed in a population of *Anartia amalthea* (Nymphalidae: Nymphalinae) inhabiting a second-growth area at Limoncocha in the eastern Amazonian rain forest of Ecuador. A capture-mark-release-recapture study was carried out to determine population size. The estimated population size using three statistical methods ranged from 100 to 255 individuals in an area 30 by 35 meters during September 4-12, 1972. More females than males were present in the population except for one day following a hard rain, when a large emergence of males occurred.

Considerable movement of marked individuals occurred between different areas of the study plot, indicating a single large population of *Anartia amalthea*. Almost half of the recaptures occurred in an area other than the area in which the butterflies were originally marked; however, only seven out of 92 recaptured individuals actually flew into all three subareas of the study site.

Social interaction observed between males and females suggested that odor, color, and motion are contributing factors in courtship behavior.

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